

A New Cryptic Species of Salamander of
the Genus *Plethodon* from the
Southeastern United States
(Amphibia: Plethodontidae)

RICHARD HIGHTON

*Department of Zoology, University of
Maryland, College Park, Maryland 20742*

ABSTRACT. — A new species of woodland salamander, *Plethodon websteri*, is described. It is a member of the *P. welleri* group of eastern small plethodons and is morphologically very similar to *P. dorsalis*, but differs from it at over 80% of 26 genetic loci as determined by electrophoresis. This represents an extreme case of genetic divergence without accompanying morphological change. The geographic range of *P. websteri* includes east central Alabama and west central Georgia with disjunct populations in Clarke County, Alabama; Winston County, Mississippi; and McCormick County, South Carolina. The ranges of *P. dorsalis* and *P. websteri* are largely allopatric, but the two have been found sympatrically at one locality in Jefferson County, Alabama.

An electrophoretic study of genetic variation in salamanders of the *Plethodon welleri* group (Larson and Highton 1978) showed that an undescribed species occurs in Mississippi, Alabama, Georgia and South Carolina. Morphologically it is so similar to *Plethodon dorsalis* Cope that there are no known standard taxonomic characters that distinguish the two species. Yet genetically they are so different that they share less than 20% of their alleles at the 26 genetic loci evaluated electrophoretically. Thus they represent a most extraordinary example of evolutionary genetic divergence without accompanying morphological change.

There is no doubt of the specific distinctness of the two species. They differ genetically from each other more than do some genera, for example *Notophthalmus* and *Taricha* (Ayala 1975). They have been taken sympatrically in Jefferson County, Alabama, and no electrophoretic hybrids were detected. The absence of diagnostic morphological characters requires that the species be diagnosed exclusively on the basis of electrophoretically detectable differences in the mobility of protein molecules. This makes it difficult to identify living or preserved salamanders. Fortunately, the ranges of the two species appear to be largely allopatric so that most individuals may be identified on the basis of geographic provenance. Moreover, in and near the zone of contact between the two

species, there is character displacement in color morph frequency, so that even in the zone of sympatry all available specimens that have been examined electrophoretically may be correctly allocated to species on the basis of color morph.

I name the new species for my friend, the late T. Preston Webster, who first called my attention to the remarkable amount of electrophoretic divergence found in southern populations of *Plethodon dorsalis* representing the new species.

Plethodon websteri, new species

Diagnosis: — An eastern small *Plethodon* of the *P. welleri* group (Highton 1962) that has virtually the same range of variation as *P. dorsalis* for all known morphological taxonomic characters, but that differs from *P. dorsalis* at most genetic loci evaluated electrophoretically. All samples of the two species are completely separable (they do not share a single common allele) at 14 of 26 genetic loci (Larson and Highton 1978): fumarase, glutamic oxaloacetic transaminase-1, indophenol oxidase-1, indophenol oxidase-2, heart lactate dehydrogenase, muscle lactate dehydrogenase, leucine aminopeptidase, malate dehydrogenase-1, malate dehydrogenase-2, peptidase-2, transferrin, and general proteins B, C and D. Most populations of the two species also are distinct at 6 additional loci: esterase, isocitrate dehydrogenase-1, isocitrate dehydrogenase-2, phosphoglucosyltransferase, phosphoglucose isomerase and general protein A. Good diagnostic loci are fumarase, indophenol oxidase-1, indophenol oxidase-2, heart lactate dehydrogenase, malate dehydrogenase-2, and protein C (the polypeptides of *P. websteri* migrate cathodally to those of *P. dorsalis*) and leucine aminopeptidase, malate dehydrogenase-1, peptidase-2 and protein B (the polypeptides of *P. websteri* migrate anodally to those of *P. dorsalis*). *Plethodon websteri* differs from *P. welleri* in the same morphological ways as does *P. dorsalis* (it has modal number of 19 trunk vertebrae compared to 17 in *P. welleri*; its belly is heavily mottled with red, white and black chromatophores compared to the black belly with small white spotting of *P. welleri*; and there is color pattern dimorphism in *P. websteri*: a red or yellow striped dorsal pattern morph and a dark brown unstriped morph in *P. websteri* compared to an unstriped brown dorsal color pattern heavily mottled with brassy flecking in *P. welleri*). The electrophoretic data and their genetic analysis are presented in Larson and Highton (1978).

Holotype: — NMNH 204814, an adult male collected 0.6 km east, 0.9 km south of Howelton, Etowah County, Alabama, on 7 January 1976 by Scott Bunting, Richard Highton, Mark Kielek and Allan Larson.

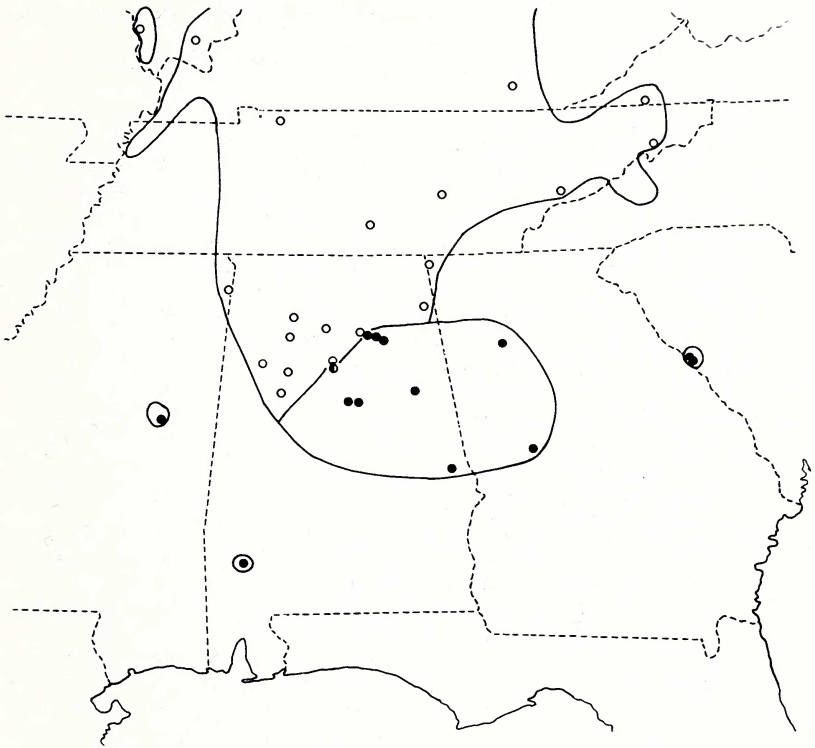


Fig. 1. Electrophoretic localities of *P. dorsalis* (hollow circles) and *P. websteri* (solid circles) in the southeastern United States. Approximate limits of the ranges of the two species are indicated. The locality in Jefferson County, Alabama where the two species are sympatric is indicated by a half solid circle.

Paratypes: — NMNH 204815-34, topotypes.

Other material: — Living individuals have been examined from all localities listed in table 1 and preserved specimens from most localities will be deposited in the collection of the National Museum of Natural History (NMNH).

Description of Holotype: — Before preservation, the length from the tip of the snout to the anterior angle of the vent was 39 mm, to the posterior angle of the vent 41 mm, and the total length 78 mm. There are 18 costal grooves (equivalent to 19 trunk vertebrae) and the vomerine teeth number 6 on each side. A red dorsal stripe with irregular edges was present in life; it is wider and brighter red on the tail than on the dorsum. The legs and sides were brown with abundant yellow and red spots and brassy flecks.

Table 1. Localities and number of *P. dorsalis* and *P. websteri* identified electrophoretically.

Species	State	County	N	North Latitude			West Longitude		
				°	'	"	°	'	"
<i>P. dorsalis</i>	Alabama	Blount	1	34	09	03	86	27	18
"	"	Cullman	1	34	10	22	86	53	31
"	"	DeKalb	3	34	23	38	85	37	38
"	"	Fayette	7	33	45	43	87	45	05
"	"	Jefferson	7	33	43	33	86	49	15
"	"	Jefferson	4	33	46	55	86	49	10
"	"	Lawrence	48	34	18	25	87	20	10
"	"	Tuscaloosa	2	33	26	38	87	29	47
"	"	Walker	7	33	42	20	87	23	22
"	"	Winston	3	34	03	30	87	20	45
"	Arkansas	Independence	23	35	52	30	91	46	26
"	"	Pope	16	35	38	28	93	04	03
"	"	Stone	45	35	59	05	92	16	02
"	Georgia	Dade	16	34	52	02	85	31	58
"	Illinois	Pope	61	37	22	54	88	40	20
"	"	Union	46	37	32	43	89	26	14
"	Indiana	Crawford	15	38	16	35	86	32	10
"	"	Parke	61	39	53	14	87	11	20
"	Kentucky	Franklin	55	38	11	24	84	52	53
"	"	McCreary	2	36	52	15	84	21	55
"	Mississippi	Tishomingo	15	34	36	23	88	10	32
"	Missouri	Taney	4	36	40	14	93	18	37
"	Oklahoma	Adair	21	35	50	13	94	39	20
"	"	Cherokee	1	35	58	03	94	48	55
"	"	Sequoyah	34	35	34	47	94	31	20
"	"	"	2	35	37	47	94	34	50
"	Tennessee	Bledsoe	32	35	38	32	85	19	55
"	"	Blount	9	35	38	20	83	44	51
"	"	"	36	35	39	56	83	47	04
"	"	Montgomery	34	36	31	00	87	30	35
"	"	Moore	7	35	20	55	86	20	30
"	"	Washington	6	36	10	32	82	31	17
"	Virginia	Scott	3	36	38	05	82	26	52
"	"	"	15	36	37	50	82	35	22
<i>P. websteri</i>	Alabama	Blount	17	34	05	12	86	20	57
"	"	"	7	34	08	03	86	23	09
"	"	Clarke	66	31	32	55	87	55	48
"	"	Cleburne	37	33	29	15	85	47	28
"	"	Etowah ¹	64	34	02	51	86	10	38
"	"	"	51	34	04	06	86	18	43
"	"	Jefferson	4	33	43	33	86	49	15
"	"	Lee	36	32	36	17	85	17	57
"	"	Shelby	9	33	21	37	86	28	38
"	"	"	1	33	22	03	86	39	49
"	Georgia	Cobb	28	33	58	34	84	34	56
"	"	Upson	91	32	47	38	84	15	30
"	Mississippi	Winston	30	33	09	10	89	02	50
"	South Carolina	McCormick	81	33	41	20	82	09	15
"	"	"	8	33	43	48	82	11	02

¹Type locality of *P. websteri*.

The chin and belly had red, white, and black pigment in the following proportions: chin 50:40:10, belly 30:60:10. It is a mature male with a rounded mental gland as in *P. dorsalis* and *P. welleri* (Highton 1962:fig. 2D).

Distribution: — *P. websteri* is known from east central Alabama and west central Georgia. Apparently disjunct populations occur in Clarke County, Alabama, Winston County, Mississippi, and McCormick County, South Carolina (figure 1).

Variation in P. websteri: — The modal number of trunk vertebrae in all known populations of *P. dorsalis* is 19. This is also true for *P. websteri* with the exception of the two samples from McCormick County, South Carolina. Both have slightly more individuals with 20 trunk vertebrae than they do with 19 (mean = 19.6 in the more southern sample and 19.8 in the more northern sample).

As in *P. dorsalis*, most samples of *P. websteri* include salamanders of both the red striped and unstriped morphs, and individuals intermediate between the two. Because of the difficulty of classifying intermediate individuals, it is impossible to objectively quantify the data on the frequencies of the color morphs. This is in contrast to several other species of the genus in which few or no intermediates between the two color morphs occur. In spite of the difficulty in classifying a few individuals, most *P. websteri* from the immediate vicinity of the zone of contact between *P. websteri* and *P. dorsalis* in Blount and Etowah Counties, Alabama are of the red striped morph, while *P. dorsalis* from nearby Lawrence, Cullman and Blount Counties are of the unstriped morph. At the locality where the two species were taken sympatrically in Jefferson County, Alabama, 8 animals of each morph were collected. Of the 11 that were examined electrophoretically, all 4 *P. websteri* are of the striped morph and all 7 *P. dorsalis* are of the unstriped morph. No intermediates are present and no genetic hybrids were found. This same kind of character displacement in color morph frequencies has been reported for contact zones of several other pairs of species of eastern small *Plethodon* (Highton 1962, 1972).

Remarks: — A photograph of a living individual from Lee County, Alabama appears in Mount (1975:133) and is presumably *P. websteri* since the locality is within the range of the species.

Although the holotype of *P. websteri* has not been subjected to electrophoretic analysis, there is little doubt that it belongs to this species. Sixty-four other salamanders from the type locality have been studied electrophoretically and all are *P. websteri*.

Additional studies of the zone of contact and/or overlap of the ranges of the two species in Alabama are needed to determine the nature of their

geographic and ecological interactions as well as the details of the color morph character displacement in that area.

No morphological differences in standard taxonomic characters used to distinguish species group taxa in the genus *Plethodon* have been detected in this pair of sibling species, but this does not preclude the possibility that a multivariate morphometric analysis might detect differential characters. Such a study would be especially interesting because of the very large amount of genetic divergence between *P. dorsalis* and *P. websteri*.

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LITERATURE CITED

- Ayala, Francisco J. 1975. Genetic differentiation during the speciation process. *Evol. Biol.* 8:1-78.
- Highton, Richard. 1962. Revision of North American salamanders of the genus *Plethodon*. *Bull. Fla. State Mus. Biol. Sci.* 6:235-367.
- . 1972. Distributional interactions among eastern North American salamanders of the genus *Plethodon*. pp. 139-188 in Holt, P.C. (ed.). The distributional history of the biota of the southern Appalachians, Part III: Vertebrates. Res. Div. Monogr. 4, Va. Polytech. Inst. State Univ., Blacksburg. 306 pp.
- Larson, Allan, and R. Highton. 1978. Geographic protein variation and divergence in the salamanders of the *Plethodon welleri* group (Amphibia: Plethodontidae). *Syst. Zool.* 27:431-448.
- Mount, Robert H. 1975. The reptiles and amphibians of Alabama. Auburn Univ. Agric. Exp. Stn, Auburn. 347 pp.

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